6 TIMBERLINE PROSPECTS AND RESEARCH NEEDS

Future timberline research will focus mainly on the response of timberline to the changing environment and possible feedbacks. In the foregoing chapter, some aspects of past and present timberline fluctuations have been highlighted, which must be considered when predicting timberline response to climatic change. Apparently, great heterogeneity as well as great regional and local variety are the main problems.

The many factors that have influenced timberline during history and those controlling timberline at present are interrelated to each other in a manifold, complex way that is hard to understand. When projecting these 'mechanisms' into a 'warmer future' we cannot be sure whether they would work in the same way as at present or as they worked in the past (Holtmeier, 2000; Giorgi and Hewitson, 2001; Holtmeier and Broll, 2005, 2007). It is still an open question which effects will result from a delayed response of high-elevation forests to a sudden climatic change (Wardle and Coleman, 1992; Lloyd and Graumlich, 1997; Peterson, 1998).

Research on carbon use of trees and its dependence from the site conditions (temperature, moisture, nutrients, etc.) in different climates needs to be continued. In this context, soil biological, soil physical and soil chemical conditions, in particular temperature and moisture regimes, decomposition and availability of nutrients, are factors that need to be more intensively studied in the timberline ecotones, in particular with respect to the many negative and positive feedbacks between the factors (see also Bekker et al., 2001). The role of soil organisms in carbon and nutrient cycles in the timberline environment has not been sufficiently considered. As the changing climate is also likely to sustainably influence also soil ecological conditions research on this issue should be intensified. In particular, the role of mycorrhiza (Section 4.3.8) within and beyond the present timberline ecotone, its interaction with tree and dwarf shrub vegetation (symbiontic and negative effects) and its dependence on physical and chemical properties of soil must be studied in detail in different timberline environments.

The present knowledge on response of the roots systems is also insufficient. We urgently need more information on cold tolerance, acclimation, and deacclimation (Bigras et al., 2001) of seedling-roots, in particular, to better understand successes or failure of seedling establishment in the harsh timberline environment (cf. Section 4.3.5).

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Systematic studies on the change of soil temperatures during the last decades (e.g., Kullman, 2007b) should be carried out in different timberline environments.

Moreover, investigations on the role of phenotypic plasticity of tree species under the influence of the harsh timberline environment (Section 4.3.11) are needed. In this context the interactions of soil temperatures and apical meristem temperatures in shaping tree life-form should be more extensively studied in different timberline environments. Moreover, investigation on hardiness of timberline trees under different climatic scenarios and nutrient supply (e.g., increased nitrogen input) would be welcome. The same holds true for photooxidative stress and photoinhibition.

At the tropical timberline, in particular, research on these issues is behind the times with a few exceptions (e.g., Beck et al., 2008) and needs to be intensified to create a more reliable basis for understanding the current situation and to speculate about the future.

Most studies have focused hitherto on the possible response of mature trees to environmental change. However, successful regeneration seems to be a bottleneck in timberline advance (cf. Section 4.3.10). Thus, there is a great need of research on the response of tree seedlings and saplings to a warming climate and its side effects. The role of facilitation for seedling establishment and survival by microtopographical structures and increasing tree population within and beyond the present timberline ecotone needs more consideration as a factor which may strongly influence the timberline spatial pattern and timberline advance.

More attention should be paid to the influence of animals, pathogens and diseases, in particular on the ecosystem level (e.g., Holdenrieder et al., 2004). The quality of mass-outbreaks of defoliation insects, for example, and their effects on timberline may change. Pathogens and diseases may increase and have stronger effects on timberline than at present. At timberline in some areas of the high-mountains in the American West, for example, white pine blister rust (*Cronartium ribicola*) is seriously affecting whitebark pines (*Pinus albicaulis*), in particular as pines stressed by blister rust are highly susceptible to attack by mountain pine beetle (*Dendroctonus ponderosae*; Keane and Arno, 1993). Stands at high altitude are usually less infected than stands at lower elevation, probably because of fewer frost-free days (Campbell and Antos, 2000). Blister rust was introduced by chance from Europe to North America in 1910 (Hoff and Hagle, 1990). Some species of *Ribes* and, more recently of *Pedicularis* and *Castilleja* have been found (McDonald et al., 2006) functioning as natural hosts of blister rust. Blister rust now has infected 25% of the whitebark pines in the Greater Yellowstone and over 80% farther north in Glacier National Park, for example (communication D. F. Tomback). Locally it destroys pine young growth also in the timberline ecotone thus acting opposite to climatically-driven timberline advance. Blister rust will probably have a lasting effect on the whole subalpine ecosystem (e.g., Arno and Hoff, 1989; Kendall and Arno, 1990; Mattson and Reinhart, 1994; Resler and Tomback, 2008; Smith et al., 2008; Tomback and Resler, 2008). In the long-term, many timberline and dry sites, currently dominated by white-bark pine, are likely to turn into hebaceous and shrub-dominated communities (Keane and Morgan, 1994, Campbell and Antos, 2000).

Forest-ungulate interactions must be studied with special regard to timberline dynamics to lay the foundations for game management in a changing environment (see also Reimoser, 2003). This holds true particularly for densely populated mountain areas where high elevation forests have a protective function.

As has been emphasized in the introduction to this book, it is differentiating the timberline phenomenon in a global perspective being a main objective of timberline research. Completing our knowledge about the present local and regional knowledge gaps on spatial and temporal structures of timberline and exploring the functional relationships behind them is an indispensable step in future timberline research rather than further focusing on 'better' coincidences between the position of timberline and certain temperatures considered to be essential to tree growth.

Thus, thorough studies are required, especially on reproduction (production of viable seeds, germination success, survival rate of seedlings, vegetative reproduction and success), on distribution pattern of tree species and ground vegetation as related to site conditions (microclimates, soil biological, soil physical and soil chemical conditions), and on site history.

These studies should be supported by physiological research in the field and in the laboratory (Figure 91), in particular on seedlings and young growth rather than on mature trees. The actual processes in and beyond the timberline ecotone can only be assessed in view of the regional climatic conditions. It is obvious from the available data that local and regional fluctuations may run counter to the long-term warming trend, as has been the case in the northern hemisphere in the period between 1940 and 1970. In this context, the interannual and annual variability of climatic factors (temperature, hygric conditions, snowmelt patterns, etc.) and their effects on regeneration and tree growth should be studied in different timberline regions. Long-term monitoring is needed of seedling recruitment as well as of disturbances (e.g., heavy storms, insect infestations, diseases, summer droughts) and resulting vegetation changes within and beyond the present timberline ecotone. Such studies should go along with manipulation experiments such as transplantation of tree seedlings to different controlled conditions or experiments on the effects of different grazing practices (e.g., reindeer). Experimental studies are essential to improve our knowledge on fundamental processes controlling tree growth and timberline dynamics.

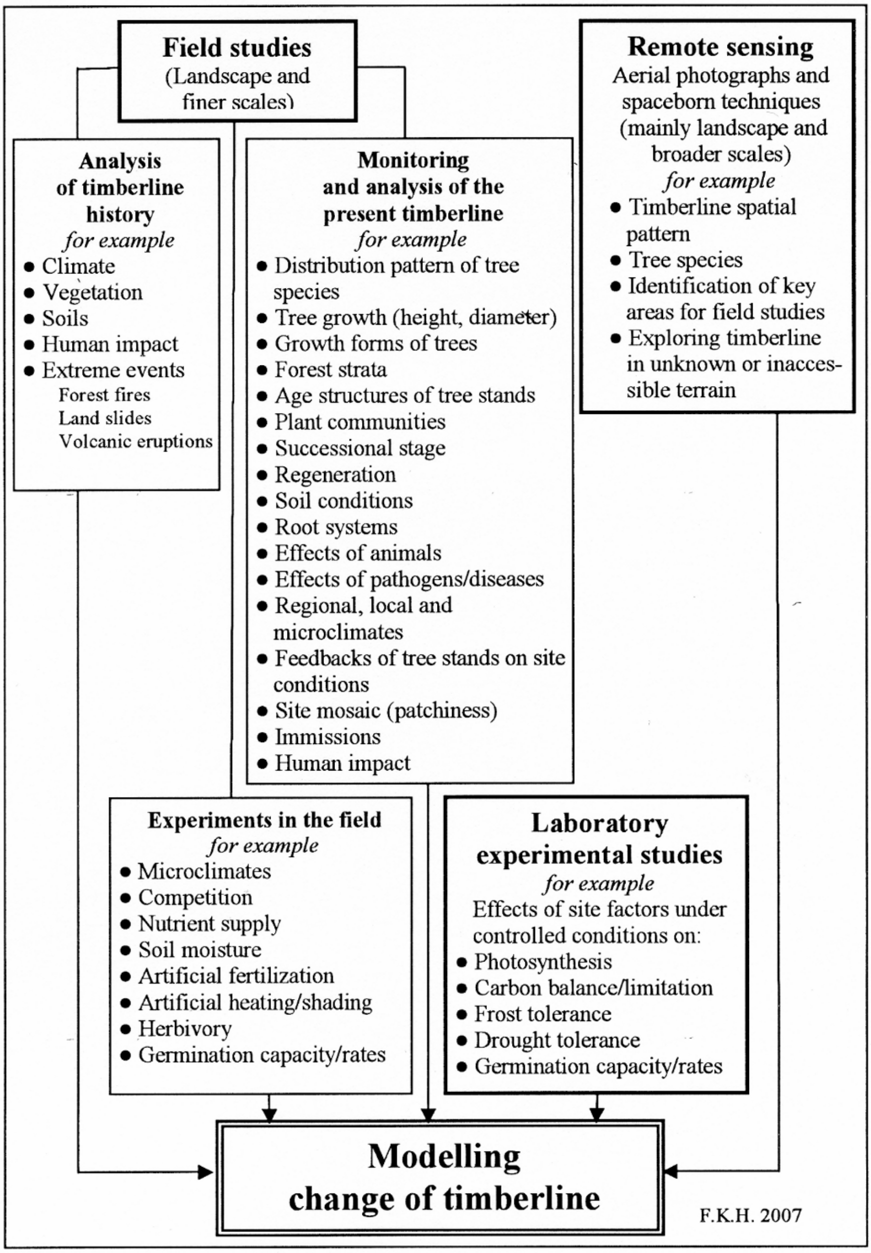

Figure 91. Basic research needed for modelling potential changes in timberline due to changing climate. Modified from Holtmeier (1993b).

Not least, the worldwide phenomenon 'timberline' should be studied with comparable methods. For long-term monitoring of the on-going changes in the timberline ecotones, the site mosaics must also be comparable as far as land-forms, parent material and soils are concerned.

During the last 2 decades, modelling the relationships between tree growth (normally mature trees) and site conditions, especially temperature, enriched CO_2 and increased nitrogen input, under changed climatic conditions has increasingly become popular in ecology (e.g., Kauppi and Posch, 1988; Ozenda and Borel, 1991; Gates, 1993; Foley et al., 1994; Bonan et al., 1995; Neilson and Chaney, 1997; Batchelet and Neilson, 2000; Rupp et al., 2001; Bekker et al., 2001). Model-based scenarios supported by geographical information systems might help to get an idea of the potential regional and local changes. This holds particularly true for the comparatively broad forest-tundra ecotone in the north, where topography and its effects on regional climates might be an essential factor controlling northward advance of vegetation boundaries. West–east oriented mountain ranges, for example, can be expected to exert a barrier effect on timberline advance to the north. This is also demonstrated by simulations on the response of subarctic vegetation to climatic warming in northern Alaska. Regardless of the degree of warming, the forest limit needed at least 1000 years to advance from its present position to the northern side of the Brooks Range (Rupp et al., 2001).

In contrast to first-generation 'equilibrium models' (e.g., Franklin, 1995; Cramer, 1997; Skre et al., 2002), dynamic vegetation models (e.g., Wolf et al., 2008) are able to represent continuous changes by including processes such as establishment, growth, reproduction and mortality, physiological adaptation and competition. Every assessment of timberline response to future climate must consider the effects of local site conditions and feedbacks of growing tree population in modulating this change (e.g., Holtmeier, 1985b, 1989, 1995a; Luckman and Kavanagh, 1998). So-called 'ground truths' are imperative as ever. Models, however, must be as simple as possible in order to work, and thus they cannot meet the complex reality, and great regional and local variety. Adding all the complexities to the existing models would increase uncertainties in the predictions (Batchelet and Neilson, 2000). In the end it will be the regionally and locally different response of timberline, which is the main characteristic of the effects of changing macroclimate on timberline (see also Luckman and Kavanagh, 1998). Models of future timberline position considering only climate as the driving factor will necessarily fail on a regional scale (Holtmeier and Broll, 2005, 2007; Rössler and Löffler, 2007).

Regional scenarios cannot be better than the data they are based on, and these data are still insufficient in most timberline areas. Thus, modern timberline research might run the risk of increasingly happening in 'cyber space'. Thus, from the present author's opinion, there is a great need for careful local and regional field studies based on a complex landscape-ecological approach that also considers the historical aspect. This might appear a little antiquated; it is however an indispensable condition for differentiating the ecological, spatial and temporal structures in the mountain timberline ecotone.

Up- and downscaling of statistically significant relationships between environmental factors and ecosystem spatial patterns and temporal structures have become popular in ecology (e.g., Curran et al., 1997). The relative importance of the factors varies by the scale of consideration (cf. Figure 2). Nevertheless, downscaling of statistical relationships existing between the timberline position and one or two obviously controlling factors (e.g., heat deficiency, lack of moisture) found that the global or zonal scale would produce simplistic scenarios that disguise the complexity and heterogeneity of the timberline phenomenon (Holtmeier and Broll, 2007) rather than contribute to a better causal understanding. Conversely, the possibility of upscaling local relationships existing, for example, between soil conditions, seedling establishment and survival, tree growth and timberline patchiness is also limited as they depend on the topographical context and thus vary locally. Timberline-specific soils, for example, do not exist (Holtmeier, 2000). Instead, mosaics of different soil types closely related to the geological substrate, varying microtopography and plant cover (e.g., dwarf shrub vegetation, grassland) are typical of the timberline ecotone (e.g., Burns, 1980; Broll, 1994, 1998, 2000; Holtmeier, 2000; Broll et al., 2007). It depends on the specific question whether and to which extent the results of studies at both broad and landscape scales can be combined.

It would be a promising strategy to compare responses of different types of timberline to environmental change: for example timberline on steep valley sides, on trough walls, on glacial moulded trough shoulders or on cirque floors, on gentle slopes with smooth microtopography and on uplifted old land surfaces (Section 4.3.9; see also Holtmeier and Broll, 2005). Response of timberline located on a gentle slope or on almost level terrain, for example, would be completely different from timberline on a steep valley side that is dissected by avalanche chutes down to the valley floor. In the latter case timberline advance would follow the slope ribs (rib and groove topography) and similar convex topography not affected by avalanches, while on gentle fjeld slopes, for example, the timberline would rise first within the shallow, wind-protected and moist valleys. On the other hand, orographic timberlines caused by steep rock walls or slope debris would probably not respond to any climatic warming, which seems important to the future forest cover, as orographic timberlines are more common in high mountains than true climatic timberlines. Remote sensing techniques such as oblique air photos and satellite imagery provide excellent tools to explore and map timberline spatial structures, timberline types (Section 4.3.9, photos and figures there; see also Allen and Walsh, 1996; Klasner and Fagre, 2002) and temporal variation even in almost unknown and inaccessible areas thus providing an unprecedented broad data base for circumpolar monitoring of timberline changes (e.g., Rees et al., 2002, there further specific literature). Interpretation, however, must be supported by field studies. Repeat photography has proven to be an excellent tool in assessing historical changes in the timberline exotone (e.g., Moiseev and Shiyatov, 2003; Roush et al., 2007).

Timberline research always is multidisciplinary. However, it will only be successful if researchers from different sciences would really cooperate (interdisciplinary research in its original sense), because the knowledge of the results of studies on single components does not automatically allow understanding the response of the forest transitions ecosystems. This is and will probably remain the most difficult problem on the way to better understanding of timberline dynamics. On the occasion of an international workshop on 'Dynamics of the Taiga-Tundra Interface' that was held in late winter 2000 in Abisko Biological station (Sweden), Robert Crawford (University of St. Andrews, Scotland) illustrated this to the timberline specialists accordingly by a remark of the playwright G. B. Shaw that was also used by W. Churchill: '*Just as America and England are two countries divided by a common language* (George Bernard Shaw), *so timberline researchers find themselves separated by the nature of a common problem – the timberline*'.